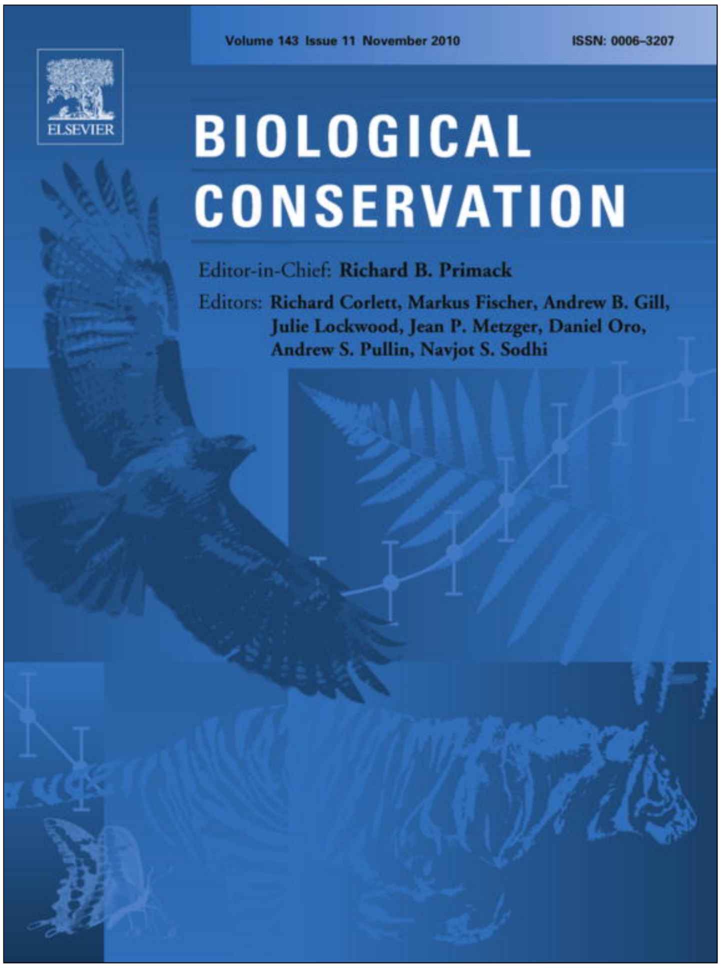

Volume 143 Issue 11 November 2010
ISSN: 0006-3207
ELSEVIER
BIOLOGICAL CONSERVATION
Editor-in-Chief: Richard B. Primack
Editors: Richard Corlett, Markus Fischer, Andrew B. Gill, Julie Lockwood, Jean P. Metzger, Daniel Oro, Andrew S. Pullin, Navjot S. Sodhi

Biological Conservation 143 (2010) 2664–2671

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Impact of season, stem diameter and intensity of debarking on survival and bark re-growth pattern of medicinal tree species, Benin, West Africa

Claire Delvaux [a,*], Brice Sinsin [b], Patrick Van Damme [a]

[a] *Laboratory of Tropical and Subtropical Agronomy and Ethnobotany, Department of Plant Production, Ghent University, Coupure links, 653, 9000 Ghent, Belgium*
[b] *Laboratoire d'Ecologie Appliquée, Faculté des Sciences Agronomiques, Université d'Abomey-Calavi, 01 BP 526 Cotonou, Bénin*

ARTICLE INFO

Article history:
Received 19 February 2010
Received in revised form 15 June 2010
Accepted 11 July 2010
Available online 13 August 2010

Keywords:
Bark stripping
Decision tool
Non-timber forest product
Ring-barking
West Africa

ABSTRACT

Bark is a greatly coveted non-timber forest product (NTFP). Its overexploitation from medicinal tree species threatens an essential source of medication for rural populations. Despite the relevance of bark, not much information is available on the ecological impact of bark harvesting. In Benin, West Africa, we investigated how various harvesting techniques affect the bark re-growth of 12 tree species and the survival of debarked trees. Trees were debarked following a combination of three factors: (i) season of bark harvesting (dry or rainy season), (ii) size class of the tree (three stem diameter classes) and (iii) intensity of debarking (seven different percentages of trunk circumference debarked). Measurements of edge growth and survival were taken every 6 months during 2 years. Ring-barking (100% of trunk circumference debarked) did not allow the sustainable exploitation of any species, while all trees with 75% of debarked circumference remained alive and produced edge growth. Whatever the bark harvesting technique, 5 out of the 12 species had a bark recovery rate below 1 cm/year, rendering the wound closure very unlikely. On the other hand, five species showed good to very good bark recovery rates (>7 cm/year) and for these species the combination of debarking factors (season, dbh and intensity) allowing the highest edge growth was determined. This experimental bark stripping revealed the complexities involved in decision-making for sustainable tree management. Studying the patterns of bark recovery rates provides a relevant tool to assess for each species the delay for achieving closure of a specific wound area.

1. Introduction

With the recent rise in concern over the sustainable management of medicinal plants, there is a need to collect and use explanatory and quantitative data on harvested species that are currently under exploitation in forests and plantations to define sustainable management strategies and avoid species extinction. Harvesting non-timber forest products (NTFPs), including medicinal plants, often alters the rate of survival, growth and reproduction of harvested individuals (Ticktin, 2004; Gaoue and Ticktin, 2007). Yet, for many species, the ecological impacts of harvesting are unknown, and this lack of knowledge hinders the identification of sustainable harvesting levels or methods (Hall and Bawa, 1993; Grace et al., 2002; Ticktin, 2004). Thus, the paucity of ecological knowledge about medicinal plants is a serious problem for resource managers (McGeoch et al., 2008). Non-sustainable harvesting not only threatens the survival of valuable medicinal plant species but also the livelihoods of communities that depend on them (Botha et al., 2004; Hamilton, 2004; van Andel and Havinga, 2008). Moreover, an excessive extraction of forest products is likely to impact negatively on the dynamics of individuals and population of the harvested species, and alter community structure (e.g. Geldenhuys and Van der Merwe, 1988; Siebert, 2004; Ticktin, 2004; Gaoue and Ticktin, 2008).

Tree bark provides the protection against external attack and desiccation and plays a key role in the transport of water and nutrients from leaves to roots through the phloem tissues. Bark removal induces internal stress and may lead to progressive or instant death depending on the extent of harvest. Ring-barking by completely removing a strip of bark around a tree's outer circumference may lead to more or less immediate tree death. However some species may survive ring-barking: e.g. cork oak (*Quercus suber*), *Eucommia ulmoides* (Li et al., 1982; Li and Cui, 1988), *Prunus africana*, *Warburgia salutaris*, *Ficus natalensis* (Cunningham and Mbenkum, 1993) or *Carapa procera* (Delvaux, unpublished data). These results have proven that it is important to test several bark harvesting treatments (including ring-barking) to determine the harvest limit. Several studies have attempted to estimate the maximum sustainable harvest rate of plant parts: leaves and ramet of *Aechmea magdalenae* (Ticktin et al., 2002), rhizomes of *Nardostachys grandiflora* and *Neopicrorhiza scrophulariiflora* (Ghimire et al., 2005), rattan of *Calamus zollingeri* (Siebert, 2004), bark of *Garcinia*

---

* Corresponding author. Tel.: +32 9 264 60 93; fax: +32 9 264 62 41.
E-mail addresses: claire.delvaux@ugent.be (C. Delvaux), bsinsin@gmail.com (B. Sinsin), patrick.vandamme@ugent.be (P. Van Damme).

0006-3207/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2010.07.009

lucida (Guedje et al., 2007). Defining a bark maximum sustainable harvesting limit for harvested species is necessary to ensure the persistence of individuals and populations.

One of the major problems a debarked tree faces is rapid and sufficient bark recovery to close the wound and provide the protection. In a recent study, Delvaux et al. (2009) were able to show that species respond to bark harvesting in various ways e.g. bark regrowth (from edge or/and from sheet), development of agony shoots (=vegetative shoots developing around a wound in response to wounding). Bark and wood recovery after debarking involve many intrinsic changes (e.g. Schmitt et al., 1997; Frankenstein et al., 2005; Pang et al., 2008). Although there is a significant interest in the bark harvesting rates (e.g. Stewart, 2003; Geldenhuys et al., 2007; Delvaux et al., 2009) our knowledge of the sustainable harvesting cycle and time elapsed between harvesting events is still limited for most tree species. Only the temporal pattern of bark recovery of *Q. suber* has already been studied and it is known that cork can only be harvested every 9–15 years. For instance, the Portuguese legislation imposes a minimum of 9 years between successive harvests (Moreira et al., 2009). We hypothesize that the bark recovery rates and thus their harvesting frequency is species-dependent.

To acknowledge consequences of tree bark harvesting and to give appropriate recommendations for a sustainable management, we hypothesized that seasons, stem diameter at breast height (dbh) and intensity of harvesting may influence bark recovery of 12 medicinal tree species. Thus the implication of the output of this study would enable the formulation of specific management strategies for each species. Specifically we addressed the following questions:

(1) How do maximum debarking rates vary between species under different intensities and timing of bark harvesting (dry vs. rainy season)?
(2) For each species, what is the delay needed to close the wound completely after bark harvesting?
(3) What are the effects of harvest seasons (i.e. dry or rainy season), size of the tree (dbh), and various harvest treatments on a specie's ability to re-grow new bark?

2. Methods

2.1. Study area and species

This study was carried out in the Forêt Classée des Monts Kouffé in central Benin (8°30′–8°52′N, 1°40′–2°27′E). This is one of the largest protected areas in the country. It covers 180,300 ha composed of woodlands, dry forests, savannas and gallery forests and located in the Sudano-Guinean region (Adomou et al., 2007). Study sites were selected in a *Isoberlinia* spp. woodland on ferruginous soils. Like most protected areas in Benin, the Forêt Classée des Monts Kouffé is somewhat degraded due particularly to encroachment for agriculture. Our sites were located away from farms. The tropical rainy season during May to October has a unimodal regime. Mean monthly rainfall during the study period in 2004, 2005 and 2006 were 138 mm, 189 mm and 165 mm respectively (ranging from 21.5 mm to 306.2 mm). The mean monthly rainfall in the dry season was 15 mm in 2006 (ranging from 2.1 mm to 42.5 mm). The annual temperature ranged from 25 °C to 34 °C and they were similar each year of the study. Rainfall and temperature data were supplied by Agence pour la Sécurité de la Navigation Aérienne en Afrique et à Madagascar (ASECNA) in Benin. The frequent and regular dry season bush fire put all living organisms in the study area under stress. Based on an ethnobotanical survey in the region (Bockx, 2004), we selected 12 medicinal tree species (Table 1) known to be debarked for primary health care by the local communities.

2.2. Experimental design

We conducted our experimental debarking in 20 sites in the dry season and 18 sites in the rainy season. For each species only healthy trees (no previous bark harvesting) were selected for the experiment. On each individual, bark was harvested from trunk at 1 m stem height. The wound was rectangular in shape with the vertical side 30 cm long and the horizontal width varying depending on the applied intensity (see below). To assess the effect of harvesting season, trees of each species were harvested both during the dry season (February and March) and during the rainy season (September and October) in 2004. We defined three classes of diameter at breast height (dbh) at which debarking occurred: 10–20 cm (dbh1), 21–30 cm (dbh2) and >30 cm (dbh3). Seven intensities (I) of bark harvesting were implemented to cover the different harvesting practices (expressed in percentage of the circumference of the debarked tree): 20% (I1), 2 × 10% (I2), 50% (I3), 2 × 25% (I4), 20% (I5), 75% (I6) and 100% (I7). For intensities I2 and I4, bark was harvested on both sides (east and west) of the trunk. For intensity I5, a square was harvested instead of rectangle. Each intensity was applied for each diameter class except for I6 and I7 which were applied only for dbh2. We marked each selected trees with coloured plastic ribbon and numbered aluminium tag. Bark was harvested from a total of 925 trees. The number of individual trees per species is given in Table 1. The reasons for differences in the number of trees per species were: (i) difficulty in finding trees with an appropriate diameter according to the species morphology; indeed, in the wild, it is rare to find examples of *Burkea africana*, *Detarium microcarpum* or *Maranthes polyandra* with a dbh >30 cm; (ii) some species (*Afzelia africana*, *Khaya senegalensis*,

Table 1
The 12 tree species used in this study. The number of individual trees observed (*N*) and the range of diameter at breast height (dbh) values are given.

Species	Family	*N*	dbh (measured) (cm)
Afzelia africana Sm.	Fabaceae (C)	68	15.6–41.7
Burkea africana Hook.	Fabaceae (C)	78	11.6–44.0
Detarium microcarpum Guill. and Perr.	Fabaceae (C)	82	13.5–45.0
Khaya senegalensis (Desv.) A. Juss.	Meliaceae	73	12.0–36.4
Lannea kerstingii Engl. and K. Krause	Anacardiaceae	48	17.0–44.9
Lophira lanceolata Van Tiegh. ex Keay	Ochnaceae	102	14.9–36.4
Mangifera indica L.	Anacardiaceae	86	12.2–47.2
Maranthes polyandra (Benth.) Prance	Chrysobalanaceae	53	12.8–35.1
Parkia biglobosa (Jacq.) R. Br. ex G. Don	Fabaceae (M)	44	14.0–49.5
Pseudocedrela kotschyi (Schweinf.) Harms	Meliaceae	93	13.3–40.4
Pterocarpus erinaceus Poir.	Fabaceae (P)	96	13.5–40.5
Uapaca togoensis Pax	Euphorbiaceae	102	12.3–48.2

(C): Caesalpinioideae; (M): Mimosoideae; (P): Papilionoideae.

Pseudocedrela kotschyi, and *Pterocarpsus erinaceus*) had been heavily harvested for timber, so that trees with dbh higher >30 cm were scarce in the study area; (iii) some species have a sparse distribution (e.g. *Lannea kerstingii*, and *Parkia biglobosa*) and finding a sufficient number of these species would have required excessive travelling and time.

2.3. Measurements

All trees were monitored a month after bark harvesting, and then every 6 months during the 2-year study period. For each tree its survival and extent of bark re-growth were recorded. A tree was considered dead when it lost all its foliage (the species phenology which was monitored throughout the study period) and if there was any sap by making a very small cut in the trunk with a knife. Bark re-growth is defined as the live tissue developing from the edge of the wound. This re-growth is called edge growth. Three horizontal measurements (cm) were made from fixed points drawn on both sides (left and right) of the wound. To calculate the total edge growth (cm), the mean value of these three measurements was added for both sides (left and right). To study the pattern of bark recovery for each species, the bark recovery rate was considered as the amount of new tissues (cm) produced over time.

Sheet growth (i.e. live tissue re-growth on the surface of the wound) was also measured; we also noted the state of the crown and the presence of agony shoots around the wound.

2.4. Data analyses

To test if species, season and intensity of bark harvesting significantly influenced tree survival after bark harvesting, we used a Generalized linear model with a binomial distribution in R (R Development Core Team 2005). To compare the variation in the different patterns of bark recovery rate among the 12 species, we classified species within four groups based on data recorded every 6 months during 2 years. These data corresponded with the measurements of edge growth expressed in cm. To test the effect of season, tree size and intensities of bark harvesting on the ability of tree species to regenerate the new bark (cm), individual scores were calculated according to 14 levels ranging from 0 to 50 cm with class intervals of 4 cm. Ordinal score levels were compared between each factor (season, dbh, intensity) for each species by a proportional-odds logit model using a polr procedure in R (R Development Core Team 2005). For this latter test, only species which presented a mean bark recovery rate higher than 4 cm/year (*K. senegalensis*, *L. kerstingii*, *Mangifera indica*, *P. biglobosa* and *P. kotschyi*) were analysed to provide relevant proposals for a sustainable management of bark harvesting.

3. Results

3.1. Effects on survival and maximum bark harvesting limits

At the start of this research, a total of 925 trees over 12 species were bark harvested. Over the 2-year study period, 72 of the 925 trees harvested died.

Regardless of seasons and treatments applied, mortality rates varied significantly between the 12 species (Fig. 1). *M. indica* was the only species for which all debarked trees remained alive and *A. africana* lost only 2 out of 66 trees. On the contrary, *L. kerstingii* was the most sensitive to bark harvesting with a mortality rate of 17.3%. *Lophira lanceolata*, *P. biglobosa*, *P. kotschyi* and *Uapaca togoensis* had similar mortality rates (Fig. 1). The five other species lost relatively few trees.

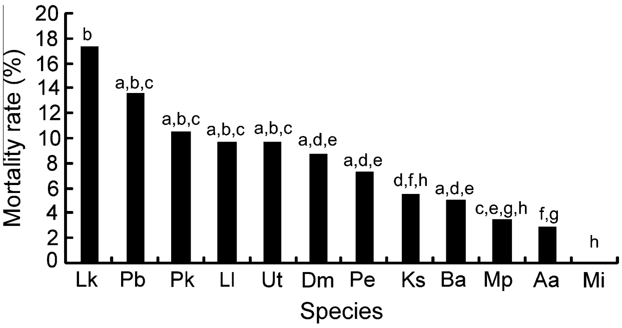

Fig. 1. Mortality rate (%) after bark harvesting for 12 medicinal tree species regardless of season and intensity of bark harvesting inflicted. Aa, *Afzelia africana*; Ba, *Burkea africana*; Dm, *Detarium microcarpum*; Ks, *Khaya senegalensis*; Lk, *Lannea kerstingii;* Ll, *Lophira lanceolata*; Mi, *Mangifera indica*; Mp, *Maranthes polyandra*; Pb, *Parkia biglobosa*; Pe, *Pterocarpus erinaceus*; Pk, *Pseudocedrela kotschyi*; Ut, *Uapaca togoensis*. Identical small letters indicate species with no significant difference at the $P \leqslant 0.05$ confidence level (GLM with a binomial distribution).

The mortality rate of harvested trees was significantly higher when harvesting occurred in the rainy season (69.4% of all dead trees) than in the dry season (30.6% of all dead trees) (GLM; $P = 0.0175$). At species level, *B. africana*, *M. polyandra*, *L. kerstingii* and *P. biglobosa* lost trees only when they were harvested during the rainy season (Fig. 1). Season of harvest did not have a significant effect on the mortality rates of *A. africana* and *U. togoensis*. *P. erinaceus*, *L. lanceolata* and *P. kotschyi* trees died in both seasons but they showed a tendency to a better survival when they were harvested in the dry season. The opposite was true for *K. senegalensis* and *D. microcarpum*.

Trees debarked at 100% (I7) were the most affected (Fig. 2) and caused the death of 44 trees (60% of dead trees). *A. africana*, *M. polyandra* and *K. senegalensis* suffered mortality only at that intensity. For all species 100% debarking resulted in death of two or more trees per species, except *M. indica* for which all individuals survived. After 2 years, 75.9% of ring-barked trees had died. For the 12 species, almost all the trees remained alive for the first 6 months. Between 6 and 18 months, 39 trees died. During the last 6 months of our experiment, the mortality was very low. The survival rate was low (24.1%) but still 14 ring-barked trees survived at least 2 years.

Trees with 50% of trunk circumference debarked (I3) had the second worst survival rate (21% of all dead trees) (Fig. 2). Under this treatment (I3), 100% of trees survived for *A. africana*, *B. africana*, *D. microcarpum*, *K. senegalensis*, *M. polyandra* and *M. indica* (Fig. 2).

After 2 years, intensity I3 led to the death of only 9.4% i.e. 15 trees out of 167 trees wounded by that intensity. The first dead trees were observed after 6 months. Most of the trees (11/15) died between 6 and 18 months. During the last 6 months of observation, only one tree was lost.

Over the 2-year study period, intensities I1, I2, I4 and I5 caused the death of only two to five trees and all trees with 75% trunk debarked (I6) remained alive (Fig. 2).

3.2. Pattern of bark recovery rates

Bark recovery rates varied greatly across the 12 species; nevertheless for all species the bark recovery rate was zero in the first month after debarking (Fig. 3). Average annual bark production varied from zero for *M. polyandra* to 10.8 cm/year for *K. senegalensis*, which were both harvested during the rainy season. Four groups of bark recovery rates were determined based on the amount of bark produced annually (Fig. 3). For Group 1, edge growth was very low with a rate of wound closure below 1 cm/year. Moreover, there was almost no increase in recovery rate over

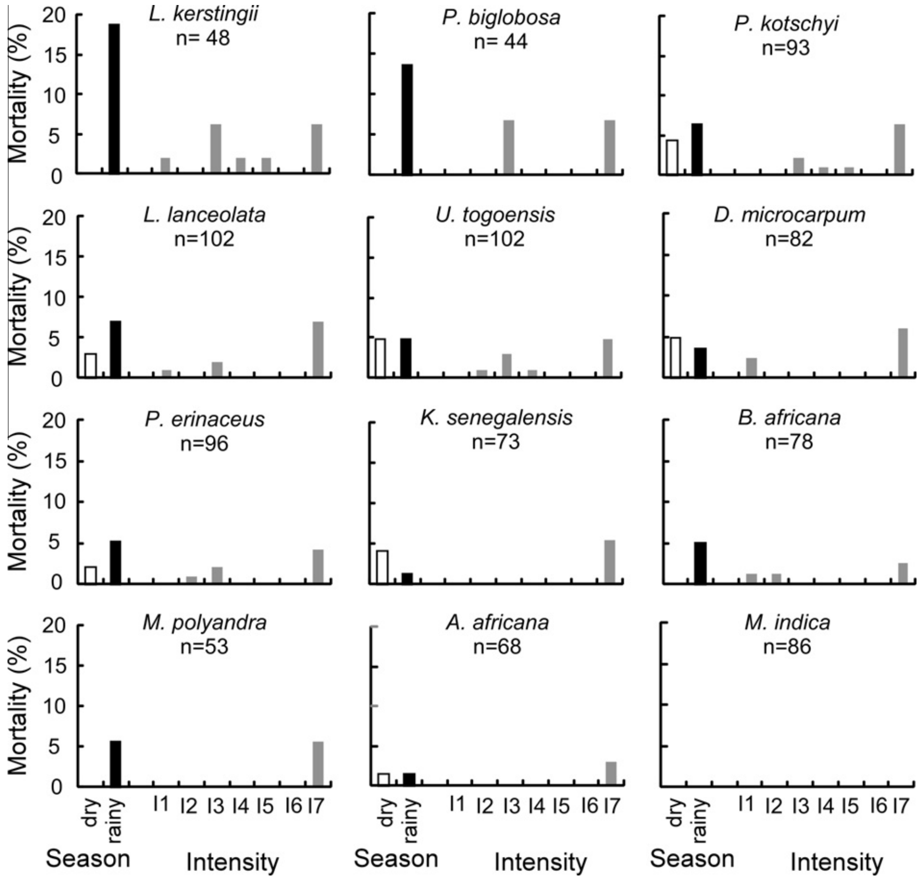

Fig. 2. Number of dead trees recorded for 12 medicinal tree species 2 years after they have been harvested during the dry season (white boxes) and during the rainy season (black boxes), and the number of dead trees recorded for 12 medicinal tree species 2 years after they have been harvested according to seven different intensities (grey boxes). *n* = number of trees harvested at the beginning of the experiment. Portion of the trunk debarked: I1 = 20% of the trunk circumference, I2 = 2 × 10%, I3 = 50%, I4 = 2 × 25%, I5 = 20% with square shape, I6 = 75% and I7 = 100%.

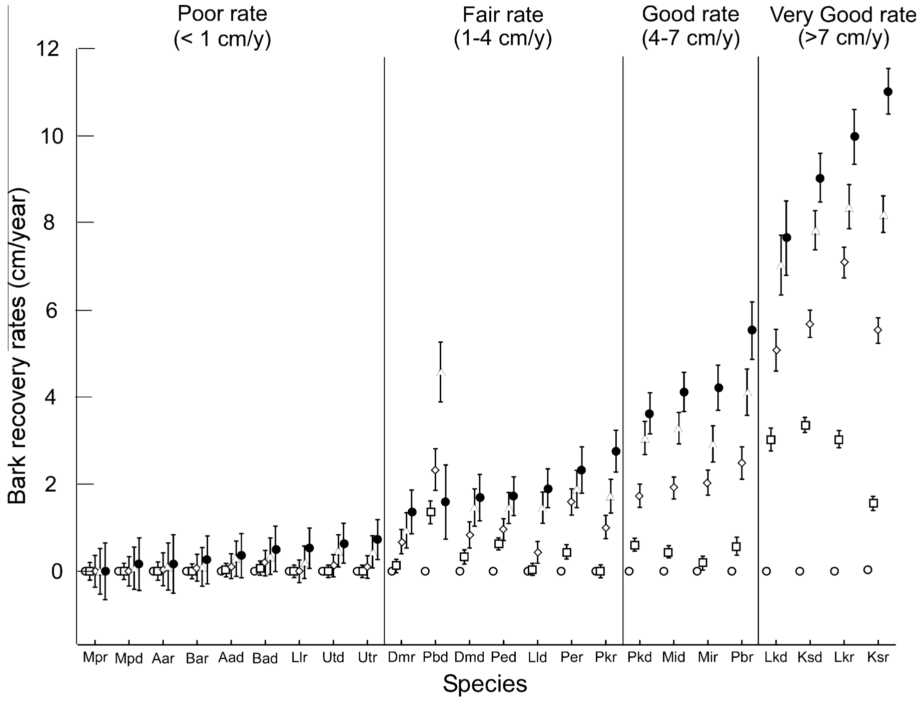

Fig. 3. Biannual pattern of bark recovery rates (mean ± SE) belonging to 12 medicinal tree species. Four groups were determined according to the amount of bark produced 2 years after debarking. See Fig. 1 for abbreviations of species. *d* = species debarked during the dry season and *r* = species debarked during the rainy season. ○ = 1st month, □ = 6th month, ◇ = 12th month, Δ = 18th month, ● = 24th month.

the 24 months of experiment. Thus, once trees had been harvested, the wound remained open. By contrast, *L. kerstingii* and *K. senegalensis*, belonging to Group 4, showed a high increase of bark recovery rate since the first 6 months after debarking. With a constantly high increment over time, these species had the best annual bark recovery rate and most of them eventually closed the wound after 24 months. For species of Group 3, edge growth really started after a 6-month delay. This is particularly true for *M. indica* debarked during the rainy season. Only for *P. biglobosa* harvested during the dry season, 65% of newly formed bark died over the course of the experiment, in the last 6 months. For this species the season of harvest substantially influenced the pattern of wound closure.

3.3. Impact of season, dbh and intensity of harvesting on bark recovery

The season of the bark harvesting (dry vs. rainy season) affected the re-growth of bark across the five selected species (Table 2). Bark re-growth of *L. kerstingii* and *P. biglobosa* was significantly higher in the rainy season than in the dry season (polr, $P = 0.019$ and $P = 0.001$ respectively). In contrast to these species, there was no significant difference between seasons of bark harvesting for *K. senegalensis*, *M. indica* and *P. kotschyi* (polr, $P = 0.121$, $P = 0.498$, $P = 0.066$ respectively).

Bark recovery rate was size-dependent except for *L. kerstingii* and *M. indica* (Table 2). No common trend was observed between the three other species. The re-growth of *K. senegalensis* varied significantly across the three dbh classes. *K. senegalensis* trees of large size >30 cm (dbh3) showed significantly higher bark regeneration than the smaller trees, i.e. dbh2 class and dbh1 class. The opposite was true for *P. biglobosa* where trees belonging to dbh1 class had significantly higher bark recovery rate than trees belonging to dbh2 and dbh3 classes. *P. kotschyi* presented a completely different response pattern. Trees with medium size (21–30 cm dbh) had a faster bark recovery than the other two dbh classes (dbh1 and dbh3) which had a similar regeneration rate.

Bark recovery rate was highly dependent on the amount of harvested bark (Table 2). For *K. senegalensis*, *M. indica* and *P. kerstingii*, intensity I6 (75% trunk debarked) yielded significantly higher bark re-growth after harvest and intensity I2 (2 × 10% trunk debarked) resulted in a significantly weaker recovery for *K. senegalensis*, *M. indica* and *P. biglobosa*. For *L. kerstingii* and *P. biglobosa*, which were not harvested at intensity I6 (75% trunk debarked), the higher edge growth appeared after the treatment of intensity I3 (50% trunk debarked).

4. Discussion

4.1. Maximum bark harvesting limits

Our study showed that when trees were debarked at 75% of their trunk circumference, they could survive at least for the next 2 years. Over the 2-year study period, 75.9% of died trees were killed by 100% trunk debarking. This result strongly suggests that the harvesting rate was not sustainable. *M. indica* was the most resistant species and could survive after ring-barking for at least 2 years after harvesting. The contrary was true for *L. kerstingii*, *M. polyandra*, *P. biglobosa* and *P. kotschyi*: all their ring-barked trees died within the 2-year period of experiment. In summary, our study shows that after high debarking intensity trees were able to survive at least for 6 months and then died.

A species may survive ring-barking, if it is able to recover the bark rapidly by producing a surface callus from the wound callus. The surface callus originates from the trunk cambium and/or from dedifferentiation of immature xylem cells (Li and Cui, 1983; Stobbe et al., 2002). Species such as *Q. suber* and *E. ulmoides* have the ability to recover the bark easily following ring-barking (Li et al., 1982; Li and Cui, 1988). The lack of sufficient sheet growth to create a new photosynthates transport structure between leaves and root may explain the mortality of trees after ring-barking. We observed trees of *K. senegalensis* and *M. polyandra* that produced sheet growth equivalent to 51.9% and 89.6% respectively of total wound surface area, although this bark re-growth was not large enough to close the wound. Moreover this bark regeneration did not survive longer than 6 months. Gaoue and Ticktin (2007), also reported that ring-barked trees of *K. senegalensis* did not survive. Similar results were also reported for *G. lucida* in Cameroon (Guedje et al., 2007). Overall, our study confirmed that ring-barking or 100% trunk debarking is not a sustainable technique, at least for the species tested. Given the biology of some species, a better alternative would be to cut individuals at 1 m height and then harvest their bark. We expect them to coppice new trunks and generate new individuals over time. Similar coppice management was already proposed by previous studies as a bark harvesting technique for *G. lucida* (Guedje et al., 2007), *Ocotea bullata* (Vermeulen, 2006)

Table 2
Influence of season, size class (dbh) and intensity of debarking on edge growth (mean ± SE, cm/year) during the 2 years following bark harvesting. Only the five species showing a bark recovery rate higher than 100 cm^2/year are tested.

	Species				
	K. senegalensis	*L. kerstingii*	*M. indica*	*P. biglobosa*	*P. kotschyi*
Season					
Dry season	9.7 ± 0.9 a	7.8 ± 0.9 a	4.1 ± 0.3 a	1.9 ± 0.7 a	3.7 ± 0.4 a
Rainy season	11.7 ± 0.8 a	10.2 ± 0.7 a	4.3 ± 0.3 a	6.2 ± 0.5 b	3.1 ± 0.4 a
Size class					
dbh1	9.0 ± 0.9 a	8.8 ± 1.0 a	3.7 ± 0.4 a	6.7 ± 1.0 a	3.1 ± 0.4 a
dbh2	12.2 ± 0.8 b	9.5 ± 1.0 a	4.3 ± 0.3 a	4.7 ± 0.9 a,b	3.7 ± 0.4 b
dbh3	15.8 ± 2.7 c	9.9 ± 1.0 a	4.3 ± 0.3 a	3.7 ± 0.7 b	3.1 ± 0.5 a
Intensity					
I1	10.6 ± 1.2 a,c	8.3 ± 0.8 a	4.8 ± 0.5 a	4.5 ± 0.8 a,b,c,d	2.9 ± 0.6 a
I2	6.8 ± 1.3 b	7.2 ± 1.1 a	3.5 ± 0.4 b	2.7 ± 1.1 a	3.2 ± 0.5 a
I3	13.0 ± 1.2 a,d	12.0 ± 1.7 a,b	4.6 ± 0.5 a	6.9 ± 1.1 b	3.2 ± 0.6 a,b
I4	8.9 ± 1.1 c	6.3 ± 2.1 a	3.8 ± 0.4 a	5.7 ± 1.7 b,c,d	1.7 ± 0.5 a
I5	14.9 ± 1.4 d	11.7 ± 0.9 b	4.5 ± 0.5 a	4.4 ± 1.3 a,c,d	3.2 ± 0.7 a,b
I6	15.2 ± 2.4 a,d	–	3.8 ± 1.0 a	–	5.5 ± 0.9 b

Identical small letters indicate no significant difference at the $P \leqslant 0.005$ confidence level (proportional-odds logit model on score level, see text). dbh1: 10–20 cm, dbh2: 20–30 cm, dbh3: >30 cm. Portion of the trunk debarked: 30 cm high and I1 = 20% of the trunk circumference, I2 = 2 × 10%, I3 = 50%, I4 = 2 × 25%, I5 = 20% with square shape, I6 = 75%.

and *A. africana*, *B. africana*, *P. biglobosa* and *P. erinaceus* (Delvaux et al., 2009).

The exact reasons why trees remained alive when their transport capabilities of water and nutrients between leaves and root were interrupted remain unknown. Thus, based on our study case where 14 trees (24.1% of ring-barked trees) remained alive after ring-barking, it would be very interesting to investigate the post ring-barking survival strategy. In our study site, *M. indica*, *A. africana*, *K. senegalensis*, *P. erinaceus* which showed cases of post ring-barking survival could be interesting study species for this purpose.

4.2. Pattern of bark recovery rates

Our experimental harvesting showed that many species had a slow response to bark removal over the 2-year study period (Fig. 3). Indeed, for *A. africana*, *B. africana*, *D. microcarpum*, *L. lanceolata*, *M. indica*, *M. polyandra*, *P. biglobosa*, *P. erinaceus*, *P. kerstingii* and *U. togoensis*, the 2-year study period was too short to provide specific management prescriptions. Estimates of recovery times are essential to develop sustainable harvesting strategies (Ticktin, 2004; Guedje et al., 2007) which is why there is a need to develop long-term studies to suggest appropriate management (Nakazono et al., 2004; Emanuel et al., 2005). Nevertheless our study of patterns of bark recovery rate offers two types of information useful for developing a sustainable management plan. We were able to determine either the time (month, year) needed to close an exact wound area, or the maximum debarked area that will be closed in the course of an exact delay. From our biannual survey of bark recovery rate we can deduce the bark recovery time for each species (Fig. 3). We consider that a bark recovery rate of 7 cm/year is the minimum growth rate necessary to close the wound completely within 2 years after bark harvesting (Delvaux et al., 2009).

For species with poor bark recovery rate such as *A. africana*, *B. africana*, *M. polyandra*, *U. togoensis* and *L. lanceolata* (Group 1), it is unlikely that they will ever recover their bark. A similar conclusion was made for *Rapanea melanophloeos* (Vermeulen, 2006). The inability to close the wound may be attributed to the variation in the anatomical composition and tissue structure of wood and bark. For instance, closure is best when the cambium "slides" over the wound surface. Consequently, if the cambium turns inward to form a callus roll, the wound may never really close (Shigo, 1986). However, this has to be confirmed through detailed study of wood production after wounding. Fair rates of bark recovery observed for *D. microcarpum*, *P. erinaceus* and *L. lanceolata* (Group 2) may be explained by the complete loss of leaves during 3–4 months from October to February. Whatever the season of debarking, the recovery occurring during the dry season (i.e. loss of leaves) showed a lower increment than during the rainy season (i.e. fully leaved). When a tree sheds its leaves, inducing cambial dormancy (Devineau, 1999; Schongart et al., 2002), no photosynthesis is taking place, and the tree has to rely on reserve energy from the previous year. When new leaves appear, they start producing more photosynthetates. Most of this energy is being used by the process of leaf formation in the early part of the period then radial stem growth occurs within a few weeks following full leaf expansion. Consequently, for deciduous species less energy is available to heal a wound over a 1-year cycle, which explains why these species (Group 2) may need at least 5 years to close the wound. The loss of 65% of newly formed bark for some *P. biglobosa* may be explained by a combination of several factors. *P. biglobosa* is wholly or partially leafless while flowering and appears to be sensitive to environmental factors such as drought (Bayala et al., 2008). Moreover, in this part of the study area bush fires are a seasonal stress for the trees. *M. indica*, *P. kerstingii* and *P. biglobosa*, species belonging to Group 3 (4–7 cm/year) would be able to close the wound within 4 years. In our study, *K. senegalensis* and *L. kerstingii* were the only two species presenting very good bark recovery rates (Group 4). The deeper root system of *K. senegalensis* trees (Ouedraogo-Koné et al., 2007), which may give better access to soil moisture and nutrients, and its deciduous phenological status (the species sheds its leaves during the dry season but they are replaced as they fall) (Devineau, 1999) may explain why this species keeps a high bark recovery rates throughout the year. Moreover *K. senegalensis* is fast growing and light demanding (Nikles et al., 2008). These intrinsic characteristics may therefore partly explain its resilience. In contrast, to the best of our knowledge *L. kerstingii* remains an enigma for us. It is a pronounced-deciduous species completely shedding leaves from November to February; thus, it is short of energy but the bark recovery rate was similar throughout the year. Moreover the bark production rate was the second best across all our studied species. Hence, the intra-specific and inter-specific differences measured over this 2-year study also indicated the influence of a genetic factor favoring or preventing wound closure.

The similarity across the 12 species is that bark recovery rate was equal to zero during the first month after debarking. Although at an anatomical level healing reactions start immediately after wounding inflicted by bark harvesting (e.g. Schmitt and Liese, 1993; Stobbe et al., 2002), no edge growth was usually measured on any tree over the first month after bark harvesting. Indeed, during this period the tree establishes boundaries within the wood present at the time of wounding to restrict the spread of microorganisms, which is vital for the protection of vascular, storage and meristematic tissues in wounded living trees. This well-known phenomenon is called compartmentalization and it results in production of tyloses into the lumen of vessels and accumulation of phenolic compounds in the parenchyma surrounding the wound (Pearce and Holloway, 1984; Shigo, 1984; Schmitt and Liese, 1994; Clerivet et al., 2000; Sun et al., 2006). Moreover, an abnormal parenchymatic cell proliferation occurs to form the wound callus (Grünwald et al., 2002; Frankenstein et al., 2005). The development of a wound callus enables early formation of protective ligno-suberized layer and wound periderm, which are necessary before dedifferentiation of new cambium, initiating the wound closure process (e.g. Oven et al., 1999; Grünwald et al., 2002; Frankenstein et al., 2005). These mechanisms occur during the first and second months after wounding (Schmitt and Liese, 1993; Oven and Torelli, 1994), thus few new tissues are produced during this period.

4.3. Influence of season, dbh and treatment

K. senegalensis, *L. kerstingii*, *M. indica*, *P. biglobosa* and *P. kotschyi* were selected because of their good to very good rates of bark recovery (Group 3 and Group 4) and thus their potential ability to support sustainable bark harvesting. Aiming at giving relevant and appropriate management advice, we provided a broad guideline for these species in terms of season and intensity of harvesting and tree size.

Our results illustrate that bark harvesting during the rainy season led to a better bark recovery for *L. kerstingii* and *P. biglobosa*. In contrast *K. senegalensis*, *M. indica* and *P. kotschyi* showed similar bark recovery irrespective of the harvesting season. The humidity of the exposed wound is the most important factor allowing the start of the bark recovery process (Li et al., 1982; Neely, 1988; McDougall and Blanchette, 1996; Stobbe et al., 2002; Mwange et al., 2003). In woodlands where the canopy is not closed and tree trunks receive the sun rays, the external humidity affects them only during the rainy season. Moreover during this season no fire occurs. Nevertheless, the variety of factors influencing the trees' response to season of bark stripping and the variable responses from different tree species do not allow for easy interpretation of experimental results that could influence harvest prescriptions (Vermeulen, 2009).

It is interesting to note that the size of the tree did not have an effect on the bark recovery rate for *L. kerstingii* and *M. indica*. The contrary was true for *K. senegalensis*, *P. biglobosa* and *P. kotschyi*, but the size class of trees showing the best bark recovery was different for each species: >30 cm, 10–20 cm and 21–30 cm respectively. This confirmed observations obtained by Gaoue and Ticktin (2007) who showed that local people harvested more bark from *K. senegalensis* trees between 35 and 95 dbh than from trees between 5 and 39 cm dbh. Vermeulen (2006) also found that smaller trees of *O. bullata*, *Curtisia dentata* and *R. melanophloeos* were more affected by an experimental bark harvesting in Southern Cape forest, South Africa. This latter experimental work confirmed inventories carried out in KwaZulu-Natal forest, South Africa, where populations of these three species were severely debarked, but only the smaller trees were not harvested (Geldenhuys, 2004). Similarly, in Cameroon, Guedje et al. (2007) showed that most of the *G. lucida* trees of 10–15 cm dbh were not harvested. Nevertheless, for a species as *P. africana* which is highly exploited for its bark, debarked trees of all sizes were found in Cameroon (Cunningham and Mbenkum, 1993), in Madagascar (Stewart, 2003) and on the island of Bioko (Sunderland and Tako, 1999).

Our study highlights that the larger the debarked surface area (I6-75% of trunk debarked) the higher the amount of bark produced per year. The contrary is also true. Overall, across five species, if a tree was debarked on both sides of the trunk (I2-2 × 10% of trunk debarked and I4-2 × 20% of trunk debarked), the bark regeneration was disadvantaged. Concerning *K. senegalensis*, *L. kerstingii* and *P. biglobosa,* the higher the tree stress (i.e. following a 75% debarked trunk), the more new tissues were produced. This could be explained by a higher hormonal activity stimulated by stress in order to restore water conductivity and thus to close the wound as soon as possible. The most likely hormones to be released are auxins and cytokinins, both being involved in cell division and shoot formation (Mohr and Schopfer, 1995). Moreover, their highly synergistic effect affects most of the growth processes of plants. In contrast, for *M. indica* and *P. kotschyi*, whatever the intensity of stress (20% or 75% debarked trunk), the trees' hormonal response in term of new tissue production is the same. Our experiment is not in concordance with previous observations following bark harvesting by local populations. Indeed, this percentage of 75% of trunk debarked was higher than what local people harvested on *K. senegalensis* in the same region in Central Benin. Indeed, in most cases they debarked less than 25% of the trunk and most of the trees harvested for more than 50% of their trunk bark were found near villages (Gaoue and Ticktin, 2007). A similar resource inventory carried out in southern KwaZulu-Natal forests showed that on average, 43% of the total bark on the main stem per tree of *C. dentata*, 31% of *O. bullata* and 24% of *R. melanophloeos* was removed (Geldenhuys, 2004).

4.4. Implication for management

Managers need to take objective decisions on the most appropriate harvest options for a particular species to ensure that bark harvesting is sustainable and to optimize socio-economic benefits from the resources used (Vermeulen, 2009). Consequently, in order to provide relevant management recommendations we used our results from the 2-year experiment based on tree responses to bark stripping according to season, dbh and intensities of debarking (Table 2). In that way, it appears clearly that *M. indica* and *P. kotschyi* do not need particular recommendations on the season, dbh and intensity of debarking because their response in term of edge growth is the same whatever the changes in these parameters. Thus for these species, the important aspect is the necessary delay to close the wound. To expect a good bark recovery rate for *P. biglobosa*, smaller trees (10–20 cm dbh) have to be harvested during the rainy season with a debarking of 50% of the trunk. In the case of *K. senegalensis* and *L. kerstingii*, we suggest larger trees to be harvested (>30 cm dbh) during the rainy season with a debarking of 75% of the circumference for *K. senegalensis* and 50% of the circumference for *L. kerstingii*. Selection of trees exhibiting rapid wound closure would therefore be a desirable practice (Neely, 1988).

Acknowledgements

This research was supported by Flemish Interuniversity Council (VLIR) Project ZEIN 2003PR278. We are grateful to Bachirou Ignintonin and Roger Gantoli for their assistance with data collection in the field. We thank Dr. François Darchambeau for his precious and efficient statistical support.

References

Adomou, A.C., Akoegninou, A., Sinsin, B., Defoucault, B., Van der Maesen, L.G.J., 2007. Biogeographical analysis of the vegetation in Benin. Acta Botanica Gallica 154, 221–233.

Bayala, J., Ouedraogo, S.J., Teklehaimanot, Z., 2008. Rejuvenating indigenous trees in agroforestry parkland systems for better fruit production using crown pruning. Agroforestry Systems 72, 187–194.

Bockx, B. 2004. Ethnobotanische Studie van Geneeskrachtige Planten in Manigri en Igbèrè, Benin. MSc Thesis, Ghent University, Ghent, Belgium.

Botha, J., Witkowski, E.T.F., Shackleton, C.M., 2004. Market profiles and trade in medicinal plants in the Lowveld, South Africa. Environmental Conservation 31, 38–46.

Clerivet, A., Deon, V., Alami, I., Lopez, F., Geiger, J.P., Nicole, M., 2000. Tyloses and gels associated with cellulose accumulation in vessels are responses of plane tree seedlings (*Platanus x acerifolia*) to the vascular fungus *Ceratocystis fimbriata f.sp platani*. Trees-Structure and Function 15, 25–31.

Cunningham, A.B., Mbenkum, F.T. 1993. Sustainability of Harvesting *Prunus africana* Bark in Cameroon: A Medicinal Plant in International Trade. People and Plant Initiative Working paper 2. UNESCO, Paris, France.

Delvaux, C., Sinsin, B., Darchambeau, F., Van Damme, P., 2009. Recovery from bark harvesting of 12 medicinal tree species in Benin, West Africa. Journal of Applied Ecology 46, 703–712.

Devineau, J.L., 1999. Seasonal rhythms and phenological plasticity of savanna woody species in a fallow farming system (south-west Burkina Faso). Journal of Tropical Ecology 15, 497–513.

Emanuel, P.L., Shackleton, C.M., Baxter, J.S., 2005. Modelling the sustainable harvest of *Sclerocarya birrea* subsp. caffra fruits in the South African lowveld. Forest Ecology and Management 214, 91–103.

Frankenstein, C., Schmitt, U., Waitkus, C., Eckstein, D., 2005. Wound callus formation – a microscopic study on poplar (*Populus tremula L. x Populus tremuloides* Michx.). Journal of Applied Botany and Food Quality-Angewandte Botanik 79, 44–51.

Gaoue, O.G., Ticktin, T., 2007. Patterns of harvesting foliage and bark from the multipurpose tree *Khaya senegalensis* in Benin: variation across ecological regions and its impacts on population structure. Biological Conservation 137, 424–436.

Gaoue, O.G., Ticktin, T., 2008. Impacts of bark and foliage harvest on *Khaya senegalensis* (Meliaceae) reproductive performance in Benin. Journal of Applied Ecology 45, 34–40.

Geldenhuys, C.J., 2004. Bark harvesting for traditional medicine: from illegal resource degradation to participatory management. Scandinavian Journal of Forest Research 19, 103–115.

Geldenhuys, C.J., Syampungani, S., Meke, G.S., Vermeulen, W.J., 2007. Response of different species to bark harvesting for traditional medicine in Southern Africa. In: Bester, J.J., Seydack, A.H.W., Vorster, T., Van der Merwe, I.J., Dzivhani, S. (Eds.), Multiple Use Management of Natural Forests and Woodlands: Policy Refinement and Scientific Progress. Department of Water Affairs and Forestry, Pretoria, South Africa, pp. 55–62.

Geldenhuys, C.J., Van der Merwe, C.J., 1988. Population-structure and growth of the fern *Rumohra adiantiformis* in relation to frond harvesting in the Southern Cape forests. South African Journal of Botany 54, 351–362.

Ghimire, S.K., McKey, D., Aumeeruddy-Thomas, Y., 2005. Conservation of Himalayan medicinal plants: harvesting patterns and ecology of two threatened species, *Nardostachys grandiflora* DC. and *Neopicrorhiza scrophulariiflora* (Pennell) Hong. Biological Conservation 124, 463–475.

Grace, O.M., Prendergast, H.D.V., van Staden, J., Jager, A.K., 2002. The status of bark in South African traditional health care. South African Journal of Botany 68, 21–30.

Grünwald, C., Stobbe, H., Schmitt, U., 2002. Developmental stages of callus formation on wound edges of broad-leaved trees. Forstwissenschaftliches Centralblatt 121, 50–58.

Guedje, N.M., Zuidema, P.A., During, H., Foahom, B., Lejoly, J., 2007. Tree bark as a non-timber forest product: the effect of bark collection on population structure and dynamics of *Garcinia lucida* Vesque. Forest Ecology and Management 240, 1–12.

Hall, P., Bawa, K., 1993. Methods to assess the impact of extraction of non-timber tropical forest products on plant-populations. Economic Botany 47, 234–247.

Hamilton, A.C., 2004. Medicinal plants, conservation and livelihoods. Biodiversity and Conservation 13, 1477–1517.

Li, Z.-L., Cui, K.-M., 1983. Vascular cambium formation in immature xylem. Kexue Tongbao 247, 249 (special issue).

Li, Z.-L., Cui, K.-M., 1988. Differentiation of secondary xylem after girdling. Iawa Bulletin 9, 375–383.

Li, Z.-L., Cui, K.-M., Yu, C.-S., Chang, X.-L., 1982. Effect of plastic sheet wrapping upon girdled *Eucommia ulmoides*. Scientia Sinica 25, 368–375.

McDougall, D.N., Blanchette, R.A., 1996. Polyethylene plastic wrap for tree wounds: a promoter of wound closure on fresh wounds. Journal of Arboriculture 22, 206–210.

McGeoch, L., Gordon, I., Schmitt, J., 2008. Impacts of land use, anthropogenic disturbance, and harvesting on an African medicinal liana. Biological Conservation 141, 2218–2229.

Mohr, H., Schopfer, P., 1995. Plant Physiology. Springer-Verlag, Berlin, Heidelberg, New York.

Moreira, F., Catry, F., Duarte, I., Acacio, V., Sande Silva, J., 2009. A conceptual model of sprouting responses in relation to fire damage: an example with cork oak (*Quercus suber* L.) tree in southern Portugal. Plant Ecology, 77–85. doi:10.1007/s11258-008-9476-0.

Mwange, K.N., Hou, H.W., Cui, K.M., 2003. Relationship between endogenous indole-3-acetic acid and abscisic acid changes and bark recovery in *Eucommia ulmoides* Oliv. after girdling. Journal of Experimental Botany 54, 1899–1907.

Nakazono, E.M., Bruna, E.M., Mesquita, R.C.G., 2004. Experimental harvesting of the non-timber forest product *Ischnosiphon polyphyllus* in central Amazonia. Forest Ecology and Management 190, 219–225.

Neely, D., 1988. Wound closure rates on trees. Journal of Arboriculture 14, 250–254.

Nikles, D.G., Bevege, D.I., Dickinson, G.R., Griffiths, M.W., Reilly, D.F., Lee, D.J., 2008. Developing African mahogany (*Khaya senegalensis*) germplasm and its management for a sustainable forest plantation industry in northern Australia: progress and needs. Australian Forestry 71, 33–47.

Ouedraogo-Koné, S., Kabore-Zoungrana, C.Y., Ledin, I., 2007. Important characteristics of some browse species in an agrosilvopastoral system in West Africa. Agroforestry Systems. doi:10.2007/s10457-007-9095-0.

Oven, P., Torelli, N., 1994. Wound response of the bark in healthy and declining silver firs (*Abies alba*). Iawa Journal 15, 407–415.

Oven, P., Torelli, N., Shortle, W.C., Zupancic, M., 1999. The formation of a ligno-suberised layer and necrophylactic periderm in beech bark (*Fagus sylvatica* L.). Flora 194, 137–144.

Pang, Y., Zhang, J., Cao, J., Yin, S.Y., He, X.Q., Cui, K.M., 2008. Phloem transdifferentiation from immature xylem cells during bark regeneration after girdling in *Eucommia ulmoides* Oliv. Journal of Experimental Botany 59, 1341–1351.

Pearce, R.B., Holloway, P.J., 1984. Suberin in the sapwood of oak (*Quercus robur* L.): its composition from a compartmentalization barrier and its occurence in tyloses in undecayed wood. Physiological Plant Pathology 24, 71–81.

Schmitt, U., Liese, W., 1993. Response of xylem parenchyma by suberization in some hardwoods after mechanical injury. Trees-Structure and Function 8, 23–30.

Schmitt, U., Liese, W., 1994. Wound tyloses in *Robinia pseudoacacia* L. Iawa Journal 15, 157–160.

Schmitt, U., Richter, H.G., Muche, C., 1997. TEM study of wound-induced vessel occlusions in European Ash (*Fraxinus excelsior* L.). Iawa Journal 18, 401–404.

Schongart, J., Piedade, M.T.F., Ludwigshausen, S., Horna, V., Worbes, M., 2002. Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. Journal of Tropical Ecology 18, 581–597.

Shigo, A.L., 1984. Compartmentalization – a conceptual-framework for understanding how trees grow and defend themselves. Annual Review of Phytopathology 22, 189–214.

Shigo, A.L., 1986. A New Tree Biology: Facts, Photos and Philosophies on Trees and Their Problems and Proper Care. Shigo and Trees, Associates, New Hampshire, USA.

Siebert, S.E., 2004. Demographic effects of collecting rattan cane and their implications for sustainable harvesting. Conservation Biology 18, 424–431.

Stewart, K.M., 2003. The african cherry (*Prunus africana*): can lessons be learned from an over-exploited medicinal tree? Journal of Ethnopharmacology 89, 3–13.

Stobbe, H., Schmitt, U., Eckstein, D., Dujesiefken, D., 2002. Developmental stages and fine structure of surface callus formed after debarking of living lime trees (*Tilia* sp.). Annals of Botany 89, 773–782.

Sun, Q., Rost, T.L., Matthews, M.A., 2006. Pruning-induced tylose development in stems of current-year shoots of *Vitis vinifera* (Vitaceae). American Journal of Botany 93, 1567–1576.

Sunderland, T.C.H., Tako, C.T., 1999. The Exploitation of *Prunus africana* on the Island of Bioko. Equatorial Guinea.

Ticktin, T., 2004. The ecological implications of harvesting non-timber forest products. Journal of Applied Ecology 41, 11–21.

Ticktin, T., Nantel, P., Ramirez, F., Johns, T., 2002. Effects of variation on harvest limits for non-timber forest species in Mexico. Conservation Biology 16, 691–705.

van Andel, T., Havinga, R., 2008. Sustainability aspects of commercial medicinal plant harvesting in Suriname. Forest Ecology and Management 256, 1540–1545.

Vermeulen, W.J. 2006. Sustainable bark harvesting for medicinal use: matching species to prescription. Trees for Health – Forever – Implementing Sustainable Medicinal Bark Use in Southern Africa. Willow Park, Johannesburg, South Africa.

Vermeulen, W.J. 2009. The Sustainable Harvesting of Non-timber Forest Products From Natural Forests in the Southern Cape, South Africa: Development of Harvest Systems and Management Prescriptions. PhD Dissertation. Thesis, Stellenbosch University, Stellenbosch, South Africa.